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MALUROSTROPHIA, A NEW GENUS OF STROPHEODONTID BRACHIOPOD FROM THE DEVONIAN OF AUSTRALIA

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Abstract

Malurostrophia gen. nov., an external homeomorph of *Leptodontella*, is considered to be derived from *Nadiastrophia* from which it differs principally in having ventrally deflected lateral margins and a dorsally deflected tongue, or from *Douvillinella* which has dorsally deflected lateral margins, but lacks a tongue. It occurs in beds of Eifelian or late Emsian age in eastern Australia in what appears to be a restricted zone. Two new species are described: *M. flabellicauda*, the type species, and *M. basilica*. Its ontogeny and the biological significance of certain of its structures are discussed. Interpretations of its feeding mechanism, the form of its lophophore and the disposition of its visceral cavity differ from previous reconstructions of strophomenid brachiopods.

Introduction

Well preserved silicified stropheodontids externally resembling the stratigraphically restricted genus *Leptodontella* Khalfin occur in abundance at Taemas, New South Wales. Recent work on a revision of the Pholidostrophiinae (Harper, Johnson & Boucot 1966) and unpublished work on forms resembling *Leptodontella* has indicated the relevance of describing this material together with material of the genus from elsewhere in Australia.

We are indebted to Prof. A. J. Boucot for encouraging us to write this paper; to him and Dr J. G. Johnson of the California Institute of Technology, and to Dr Charles Harper of the University of Oklahoma for generously sending us copies of their manuscript on the Pholidostrophiinae in advance of publication; to Mr B. Chatterton for making available certain specimens from Taemas; to Dr G. Arthur Cooper for the loan of the dorsal interior of *Leptodontella caudata* described by Williams (1953) and the specimen reproduced on Pl. 50, fig. 13; to Prof. H. B. Whittington for the specimen on Pl. 50, fig. 11; to Mr Leo Seeuwen and Mr Philip Bock for the photographs of plates 47-49; to Miss J. Shepherd for the draughting of text-figures; to Dr M. J. S. Rudwick and Dr J. G. Johnson for critical comment; and to Dr D. E. Thomas, Director of Geological Survey, Mines Department, Melbourne, for permission for one of us (J.A.T.) to publish. The views expressed are entirely our own responsibility.

Systematic Description

Family Stropheodontidae Caster 1939

Genus **Malurostrophia** gen. nov.

Derivation of Name: Allusion to the Maluridae, the Australian fairy wrens, notable for their elegant erect tails.

Type Species: *Malurostrophia flabellicauda* sp. nov.

DIAGNOSIS: Unequally parvicostellate stropheodontids having a thin body cavity; valve margins sharply geniculate and ventrally directed except for a prominent dorsally directed tongue in the anterior margin, and reflexed lateral margins in front of the ears in some large specimens. Pedicle valve with an anteriorly bilobed rhomboidal diductor field and strong muscle bounding ridges; in adults marginal ridge pronounced laterally, rarely continued across the inner surface of the tongue. Brachial interior with roundly triangular muscle scars bounded laterally by high ridges, and divided medially by a shallow furrow; medial pair of adductor scars situated well back and lying astride the transmuscle ridges (= 'brace plates' of most recent literature. It is argued below in the section on Functional Morphology that these structures did not support the lophophore: the term is therefore misleading.) The transmuscle ridges are continued forwards and increase abruptly in height in front of the muscle scars; low breviseptum present in front of muscle scars; in large specimens shell thickening forms an antero-medial prominence over and a little in front of the distinct pit on the exterior of the brachial valve; a corresponding pit occurs on the interior of the pedicle valve; hinge line denticulate for approximately half its length; cardinal process lobes disjunct; socket plates present.

GENERIC RELATIONSHIPS: The systematic division of the Stropheodontidae is at present quite unstable; the extent of the instability can be gauged from a comparison of the genera included in the Pholidostrophiinae by Williams (in Moore 1965) and Harper *et al* (1967). For this reason we have not discussed the assignment of *Malurostrophia* to a subfamily, but have been content to indicate relationships with existing genera.

Though the external shape, thin body cavity, and ornament of *Malurostrophia* are very similar to those of *Leptodontella* Khalfin, there are reasons for believing that the relationship between these genera is more remote than such similarities might indicate. *Leptodontella* has very flabellate diductor scars in the pedicle valve and correspondingly widely spaced 'brachial ridges' in the brachial valve; it has no true socket plates and no transmuscle septa; it has a median ridge running up to the base of the cardinal process, the lobes of which are not as sharply disjunct as those of *Malurostrophia*; its hinge line is completely denticulate; and it does not develop a sharp prominence on the median anterior of the brachial valve. We consider the external similarities of these two genera to be adaptations to feeding in a similar orientation with respect to the substrate, a phenomenon also known in the leptaenids (see section on Functional Morphology below).

Comparison may also be made with *Douvillina* Oehlert, as interpreted by Williams (1953, and in Moore 1965); their external shapes are entirely different. *Douvillina*, in common with many stropheodontids, has a strongly and evenly convex pedicle valve, a closely fitting concave brachial valve, and consequently a thin body cavity. Note that these differences involve the whole shell and not only the marginal deflexions. Internal similarities include strong lateral bounding ridges in the muscle field of the pedicle valve, well developed transmuscle septa, a vestigial chilidium, disjunct cardinal process lobes and strong lateral muscle bounding ridges not everted posteriorly; the socket plates and the breviseptum are obsolescent, and the cardinal process is differently oriented. We conclude that the differences are more significant than the similarities and that there is no close relationship between the genera.

The muscle scars in the pedicle valve of *Malurostrophia* are reminiscent of those of *Shaleria* Caster in that they are long and narrow, bounded laterally by strong ridges that are posteriorly everted, and deeply cleft in front by muscle bounding ridges. Further, the shallow body cavity, ornament, form of the pseudodeltidium and ventral process, and the denticulation are similar in the two genera. The shape of the muscle bounding ridges and the transmuscle septa, and the lack of a breviseptum and socket plates, do not confirm any suggestion of relationship. *Telaeoshaleria*, now removed from proximity to *Shaleria* (Harper *et al* 1966) has a somewhat similar interior in the pedicle valve, strong transmuscle septa and a breviseptum not unlike those of *Malurostrophia*, but it is deep bodied, has a powerful marginal ridge in the brachial valve, and cardinal process lobes of a most distinctive pattern.

Douvillinella Spriestersbach (1925) has been used to embrace resupinate Devonian douvillinids. Its late Emsian type species, *Douvillina filifer* Schmidt (1912) has cardinalia and musculature in the brachial valve similar to the present genus, but has an essentially subcircular muscle field in the pedicle valve composed of two broadly ovate to rounded trigonal adductor scars. This, the resupinate character, and the absence of a dorsally deflected tongue are sufficient to separate them; but the similarities are such that *Malurostrophia* could conceivably have been derived from *Douvillinella*, a genus not yet known from Asia or Australia.

It is with the genus *Nadiastrophia* Talent, from the Lower Devonian of Victoria and the Middle Devonian of China, that we consider *Malurostrophia* has the greatest propinquity. They both have unequally parvicostellate ornament, a shallow body cavity, an extended hinge, elongate anteriorly cleft muscle scars with everted lateral bounding ridges in the pedicle valve, strong transmuscle septa and lateral muscle bounding ridges in the brachial valve, peg-like cardinal process lobes which are similarly oriented, blade-like socket plates set in similar positions, and a distinct breviseptum. The lateral margins of the valves, however, are directed in opposite senses, a feature which gives the two genera a misleading impression of disparity. They also differ in the relative proportions of the adductor scars in the brachial valve, the more extended denticulation of the hinge and in the apparent absence of vascula dentalia in *Nadiastrophia*. These differences are considered to be minor. In view of their stratigraphic positions, it is concluded that *Malurostrophia* was derived from *Nadiastrophia*. It is noted that although Talent (1963, p. 62-3) considered *Nadiastrophia* to be allied to the shaleriinids, Harper *et al* (1967) have transferred it to the Pholidostrophiinae, an assignment we find difficult to accept.

Malurostrophia flabellicauda sp. nov.

(Pl. 47, fig. 1-16; Pl. 48, fig. 1-20; Pl. 49, fig. 1-8; Pl. 50, fig. 8-10; Fig. 1-10)

TYPES: Holotype 14620; paratype 14614-19, 14621-67, 14982-93, all Australian National University.

DESCRIPTION: **Exterior of pedicle valve.** Earliest growth stages of pedicle valve having a relatively broad median furrow, but shell overall convex; slight medial ventral deflexion beginning at length of 4-5 mm and increasing rapidly in height, width of deflexion showing considerable variation; ventral deflexion of entire shell margin beginning at this stage, followed later by reversal of deflexion of median sector and its positive allometric growth in a dorsal direction. Hinge of earliest growth stages not observed; at shell width of 3-4 mm hinge extremities subrectangular, then becoming slightly alate, alation increasing with further growth. Ornament unequally parvicostellate throughout; median furrow and median rib present at earliest stages (for arrangement of primaries see Pl. 47, fig. 2, 4, 7); secondaries tending to be introduced at ⅓ to ½ length of the valve, attaining same size as primaries; tertiaries of more or less uniform size, all apparently intercalated; uniform lirae cover the shell surface between the costae and costellae, increase by intercalation, and number 4-5 per half mm at the geniculations; ornament on tongue stronger than elsewhere, with quite large costellae inserted and reaching maximum size within about 1 mm after insertion. Cardinal area gently concave in adults; outline of delthyrium not clearly distinguishable; pseudodeltidium bearing a high median fold. Pedicle foramen occupies the tip of the umbo and is 0·07-0·1 mm in diameter at the time of pedicle atrophy, i.e. a little before the period of initial shell geniculation; pedicle tube passes through the shell at a very low angle to the external shell surface (Pl. 48, fig. 17-18); no sign of pedicle sheath, though its apparent absence could be the result of weathering.

Exterior of brachial valve. A small protegular node is present and is extended forward for *c.* 1 mm as a vague ridge from which the primary costae are derived (Pl. 47, fig. 1, 3, 5). Cardinal area linear; notothyrium triangular, higher than wide; chilidium indistinct, variable in shape but often with a node at the apex, a concave ventral edge (which is sometimes slightly raised), and a slightly depressed central region (Pl. 48, fig. 4; Pl. 49, fig. 3).

Interior of pedicle valve. Ventral process present early as a very faint mound, beginning to develop at the same growth stage as the tongue, merging anteriorly into a pair of ridges bounding the postero-lateral edges of the adductors; process pits deep. Muscle fields of juveniles relatively wide; muscle scars at shell width of 5-6 mm bounded postero-laterally by a slight thickening; strong postero-lateral muscle bounding ridges rising above shell surface are present when the marginal deflexion develops (Pl. 47, fig. 12), but the antero-lateral and anterior edges of the muscle scars, though distinguishable, are not defined by ridges. In adults, the outer edges of muscle scars are invariably defined by ridges or plates of a very distinctive shape, the postero-lateral portions being massive and having their dorsal edges bent sharply outwards forming a platform-like structure (Pl. 48, fig. 15; Pl. 49, fig. 4-7); the muscle bounding ridges drop sharply in height in front of this structure, gradually diminishing to the anterior edge of the scars; widest part of scars at about their mid-length and just anterior to the 'everted' part of the bounding ridges; each diductor scar tapered anteriorly, rounded in younger individuals, produced to a blunt point in the largest specimens; inner edges of diductor scars bounded by weak ridges; adductor scars ovate to semi-cordate, slightly platformed. In two juvenile pedicle valves 3 mm and 3·5 mm long and 5·5 and 5·2 mm wide respectively, the medial muscle-bounding ridges are high and pustulose, with very feeble expression of the lateral ridges; these are quite strongly expressed in our remaining material 11 mm wide or larger. A thickened ridge extends around the valve inside the deflexion, merging into a triangular postero-lateral platforming of the inner edges of the ears. It usually dies out against the tongue, but in some specimens continues onto the inner surface of the tongue, and very rarely completely traverses it; the marginal ridge is initiated soon after deflexion of the valve edge (Pl. 47, fig. 12) and continues to develop throughout life, its dimensions depending on the age of the individual (Pl. 47, fig. 13-15; Pl. 49, fig. 4-8). A distinct groove or channel (vasculum dentalium) runs from the body cavity to each of the cardinal extremities, lying in front of and at a low angle to the hinge; it is present in young specimens, becoming particularly prominent in adults bearing wide ears; it is sometimes vaguely divided by an indistinct longitudinal ridge (Pl. 49, fig. 6) and is markedly shallower where it crosses the marginal ridge (e.g. Pl. 47, fig. 13-15; Pl. 49, fig. 6-7). Denticles are apparently absent in specimens 5 or 6 mm long; 7 to 11 denticles are present on each side of the umbo and occupy a little more than half the length of the hinge at the stage where marginal deflexion begins; in adults there are up to 22 denticles on either side of the umbo; the denticles are borne on a ridge, and increase gradually in size from the extremities towards the muscle-bounding ridges, then rapidly diminish towards the midline (Pl. 47, fig. 14; Pl. 49, fig. 5-7).

Articulation of valves as follows: the socket plates of the brachial valve fit into a socket in the pedicle valve lying between the inner edges of the tooth plate and the outwardly deflected edges of the muscle-bounding ridges; the broad ridges running antero-laterally from the cardinal process of the brachial valve then lie flat against the outwardly deflected edges of the muscle-bounding ridges. The denticulation of the brachial valve is actually a series of sockets lying in a groove, that of the pedicle valve being a series of denticles arranged on a ridge, the groove and ridge in both cases extending laterally beyond the denticulation and forming a weakly ginglymoid type of dentition.

Mantle canal system not clearly impressed on the shell in available specimens except for the vasculum dentalium which passes into a strong groove extending towards the ears and lying almost parallel to the hinge. The inner surface does however bear a radiating series of grooves corresponding to the ribs of the exterior of the shell; these become progressively lost toward the muscle scars but are retained or become intensified on the deflected margins and on the inner surface of the tongue where they are particularly densely packed (Pl. 47, fig. 16). The internal expression of surface ornament on the body of the shell is highly variable, some geniculate specimens showing the costae, the costellae and the lirae, the latter being outlined by rows of pustules. In the majority of specimens there is no differentiation on the inner surface between coarser and finer ornament on the body of the shell; in larger specimens the pustules become more random in distribution with a general tendency to become finer towards the geniculate portions. The pustules are often noticeably hollow.

Interior of brachial valve. Hinge line consisting of a dental groove extending to the cardinal extremities, denticulate for approximately half its length. Cardinal process lobes disjunct, circular to ovate in cross-section, each becoming distinctly bifid in specimens 12 mm or more in width, diverging between 40° and 60° from each other, and directed posteriorly at 65° to 70° to the floor of the valve. Socket plates blade-like, aligned at *c.* 20° to the hinge line. Lateral muscle bounding ridges typically arcuate and pustulose, joined to the posterior thickened shelf paralleling the hinge line, but not joined or only feebly joined to the transmuscle septa; these ridges lie with their ventral edges immediately opposite the everted edges of the muscle bounding ridges of the pedicle valve. A low, vaguely defined arcuate and pustulose ridge (Pl. 48, fig. 7) runs forward from the muscle bounding ridges in adults (= the lateral brachial ridge of Harper *et al*). Adductor scars roundly triangular in outline and divided by a shallow median furrow; lateral scars sausage-shaped in outline, and spread well up to the lateral ridges; median scars tear-shaped with their posterior edges bluntly pointed and situated a short distance in front of the posterior edge of the lateral scars, their inner edges close to the mid-line of the shell. A transmuscle septum bisects each median adductor scar and increases abruptly in height on emerging from its anterior edge; these septa are most obvious beneath the scars in young specimens, but become progressively more obliterated with age by the deposition of muscle callus (Pl. 48, fig. 14, 5, 2, 3 show specimens of increasing age). In young specimens transmuscle septa terminate abruptly anteriorly, but in adults low anterior extensions converge to outline a canoe-shaped structure divided by a low median breviseptum and rising to a low eminence at a point 0·6-0·7 of the distance from the posterior shell margin to the geniculation. Surface anterior to this structure has a pronounced rounded ridge rising up the geniculate area to a pointed pyramidal prominence corresponding to a distinct but vaguely defined pit on the exterior, the point where an abrupt reverse in sense gives rise to the tongue.

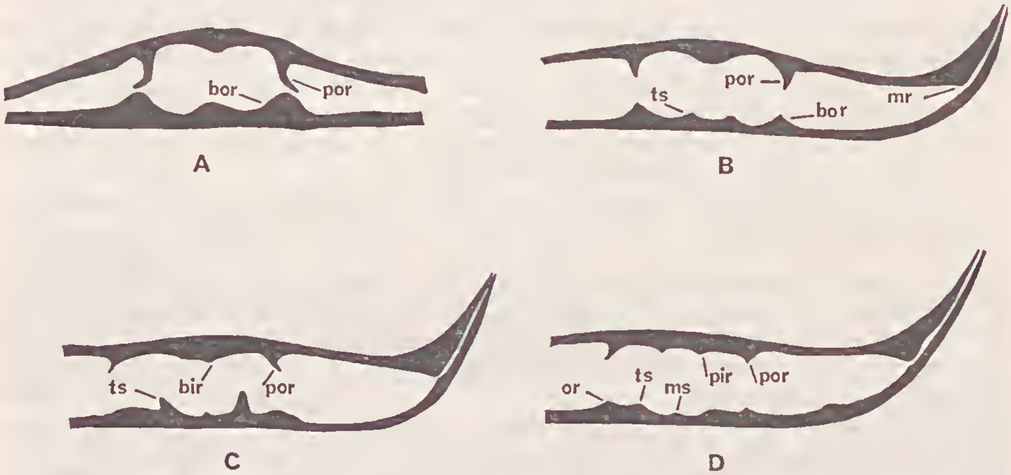

FIG. 1—Serial sections across specimen ANU 14992. Intervals between sections are as follows: 0·4, 0·8, 0·4 mm. bor = outer muscle ridge in brachial valve; c = excrescence; mr = marginal ridge; ms = breviseptum, or = 'lateral brachial ridge'; pir and por = inner and outer muscle bounding ridges in pedicle valve; ts = trans-muscle septum.

Mantle canal system usually not impressed, but details can be reconstructed from three well preserved individuals (Pl. 48, fig. 6-10; Fig. 2). A clear vasculum cardinalium passes into a prominent groove on the ears, directed at 4°-10° to the hinge. This lies opposite the comparable groove on the pedicle valve. There is no sign of saccate vascula genitalia, and this structure can best be described as pinnate. The vascula myaria are many branched and serve the water intake sector of the shell edge. The ramifying vascula media serve the entire deflected median sector.

DISCUSSION: A few points in the above description need further comment.

The outlines of the species are very variable as can be seen from the plates, the plots of dimensions (Fig. 3-7; Table 1), and the figures. It should be noted that because of the geniculation the dimension 'length' is not a reflexion of the amount of growth in a plane at right angles to the hinge. The curvatures shown by the plot in Fig. 3 are due partly to the early allometric growth of the hinge, and partly to this artifact. Estimates of total width have frequently to be made from specimens with broken or partly silicified ears, but this is unlikely to involve any considerable error.

Measurement of the distance between the hinge-line and the point of the anterior node of forty-five specimens gave a mean of 4·91 mm, a standard deviation of 0·69 mm, and a total range of 3·7-7·0 mm, though only three individuals have values >5·5 mm and one <4·0 mm. This dimension is independent of age and is a useful one in distinguishing between the two species described herein.

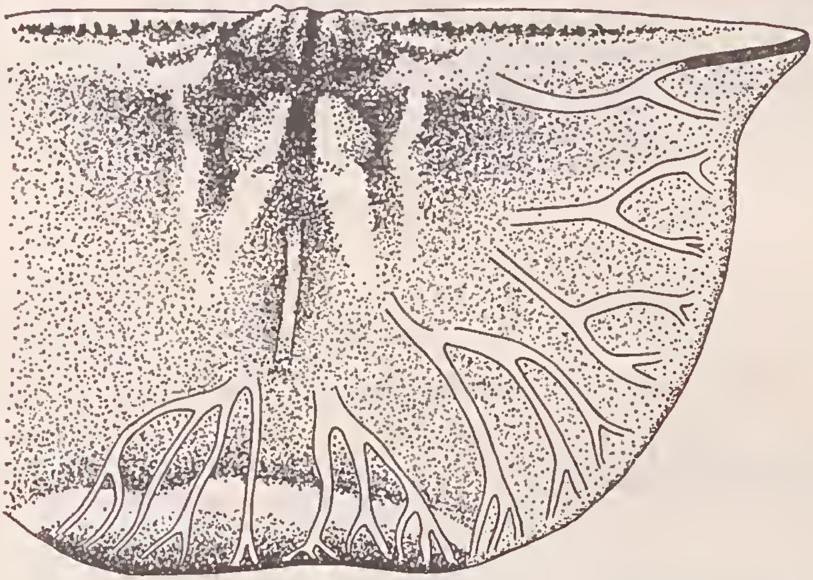

FIG. 2—Reconstruction of the mantle canal pattern in the brachial valve of *Malurostrophia flabellicauda*, based mainly on ANU 14984 and ANU 14619. (Compare with Pl. 48, fig. 6, 7, 9, 10.)

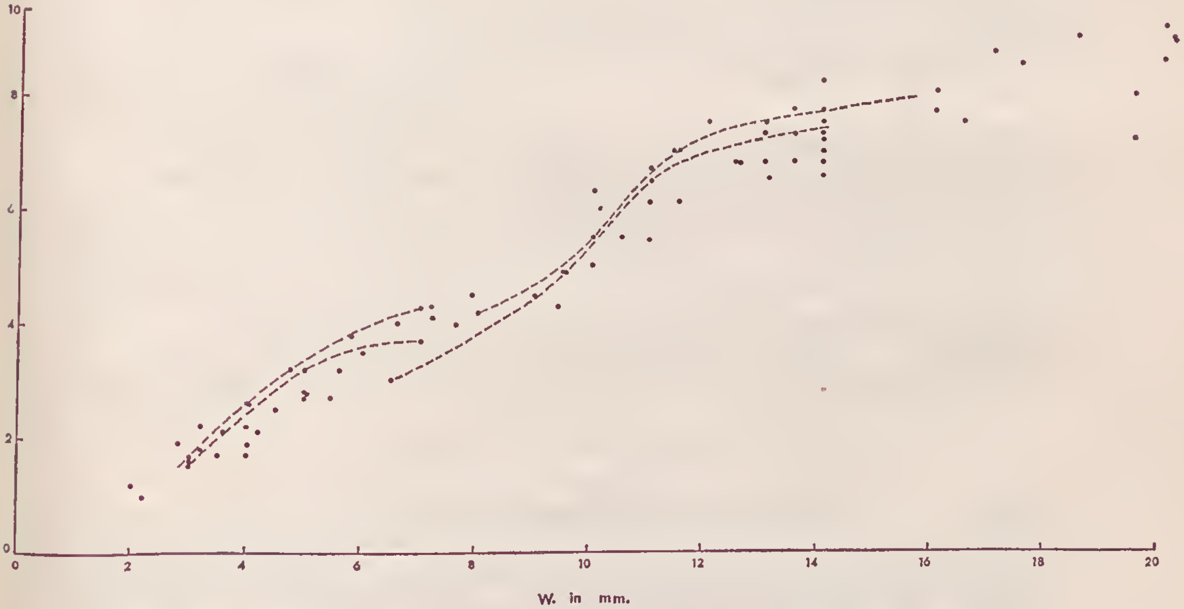

FIG. 3—Plot of Total Shell Length against Total Shell Width. The dotted lines indicate growth patterns of four specimens.

Width of the Fold also is very variable. It varies with age. For this reason it is shown in Fig. 4 and 5 plotted against the Length of the Muscle Scars in the Pedicle Valve, a dimension which apparently shows linear increase with age, and against Total Shell Width. The growth lines suggest also that the latter increases linearly with age beyond the stage where the fold develops. Both show a wide scatter; the value of the correlation coefficients are r = +0·45 (n = 31) and r = +0·61 (n = 31) respectively.

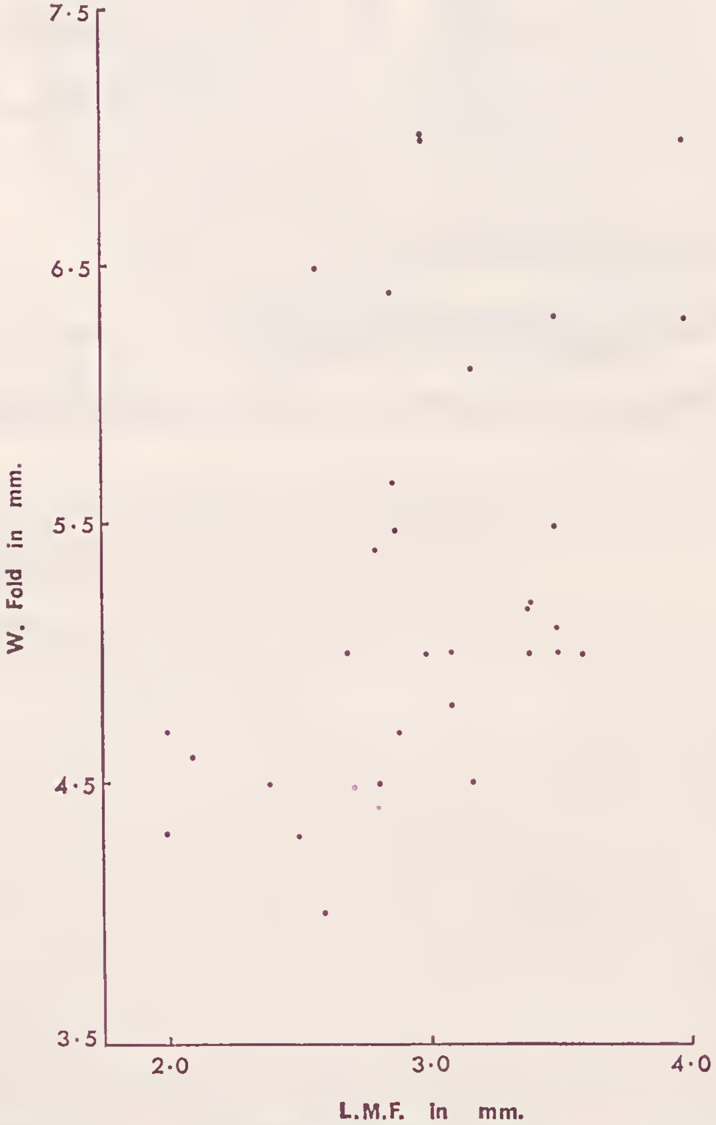

FIG. 4—Plot of Length of Muscle Field in Pedicle Valve against Width of Fold of *Malurostrophia flabellicauda.*

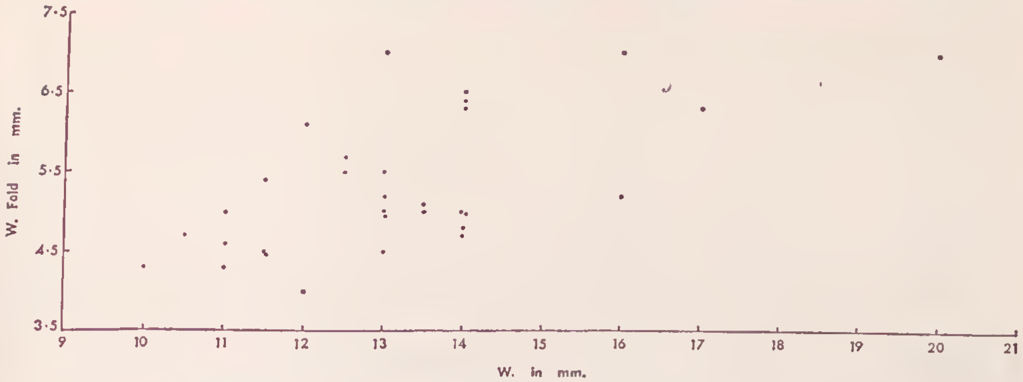

Fig. 5—Plot of Total Shell Width against Width of Fold of *Malurostrophia flabellicauda.*

The plot of Length of Muscle Scars against Width of Muscle Scars (in the pedicle valve) exhibits a considerable range of variation. The relatively narrower specimens usually fail to show a bulge in the outline of the scars near their mid-length. The valve of r is +0·79 (n = 41).

Two further features, variations in which profoundly modify the overall appearance of the shell, are the amount and angularity of the ventral median deflexion that produces the median node (cf. Pl. 47, fig. 6 and 7; Pl. 48, fig. 20), and the time of onset of the reflexion of the margins in front of the ears (cf. Pl. 47, fig. 14-15; Pl. 48, fig. 15, 16, 20 with Pl. 49, fig. 6 and 7).

Finally, the adductor scars in the brachial valve are poorly differentiated into anterior and posterior pairs until the late adult stage. The anterior scars lie astride the posterior ends of the transmuscle septa which are only partially resorbed. At the late adult stage, however, resorption is greatly increased, the septa show an abrupt increase in height at the edge of the muscle field, and the anterior adductor muscles build distinctly platformed scars.

Distribution: Silicified specimens occur in great abundance in limestones of the *Receptaculites* Limestone at Bloomfield Station, Taemas district, near Yass, and in the Crinoidal Limestone, Hume Park, near Yass, N.S.W. (for stratigraphy see Browne 1959). It occurs in relative abundance, but less well preserved, in the *Calceola* band of the lower Murrindal Limestone on the crest of the ridge running east from Rocky Camp, Buchan, Victoria (for stratigraphy see Teichert & Talent 1958). A poorly preserved specimen of what may be the same species occurs in collections made by the Bureau of Mineral Resources, Geology and Geophysics, at locality B76, Ukalunda Beds, Ukalunda, Queensland. On present information the best age estimate for all these localities is in the range late Emsian-Eifelian.

Malurostrophia basilica sp. nov.

(Pl. 50, fig. 1-7)

Description: **Exterior of pedicle valve.** Hinge extremities broken on available specimens, but obviously alate in the unbroken state. Pedicle valve more or less planar with a ventral deflexion of the entire shell margin beginning at about 9 mm, followed by reversal of deflexion of the median area at about 10 mm from the umbo to form a dorsally directed rounded tongue. Tongue about 5 to 6 mm wide. Orna-

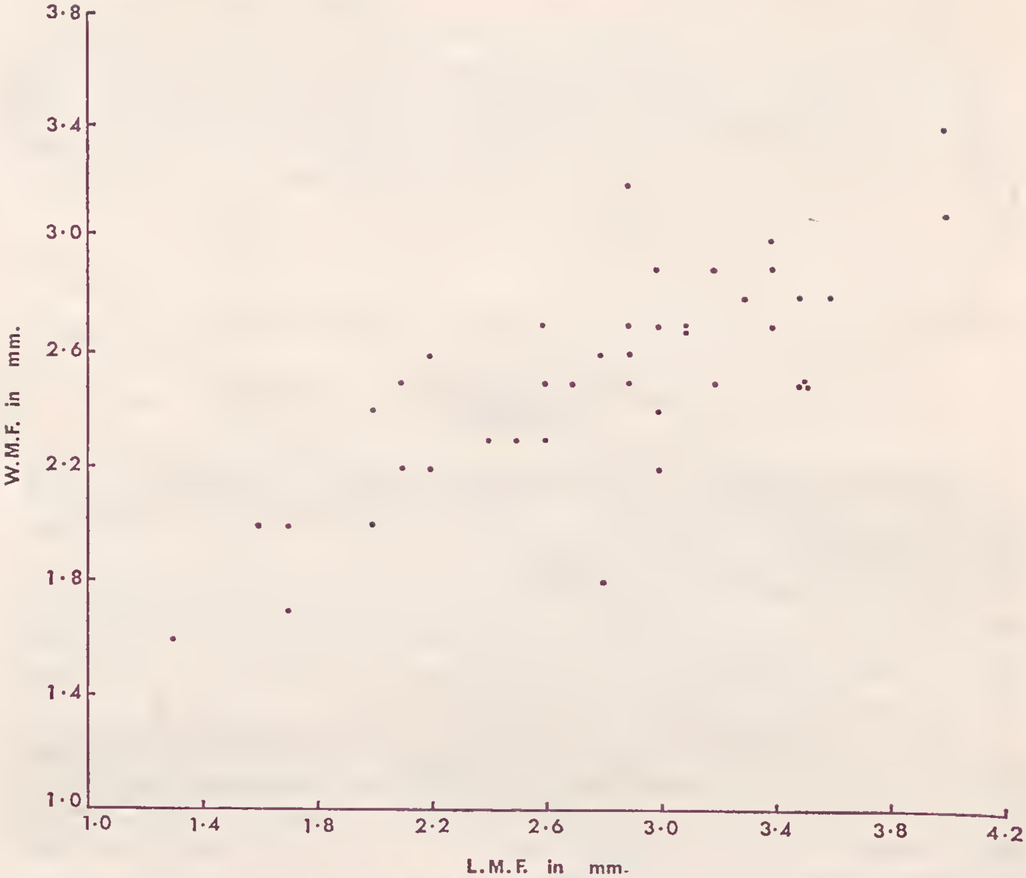

FIG. 6—Plot of Length of Muscle Field against Width of Muscle Field (in the pedicle valve) of *Malurostrophia flabellicauda.*

ment parvicostellate throughout, but with primaries more closely spaced (5 or more in 3 mm) and more numerous at any given growth stage than in *M. flabellicauda*, and with stronger secondaries giving, on first glance, the impression that the ornament is costellate rather than parvicostellate; ornament on tongue costellate. Cardinal area gently concave.

Interior of pedicle valve (Pl. 50, fig. 7). Ventral process merging anteriorly into a strong pair of ridges bounding the adductor field. Diductors bounded by strong muscle-bounding ridges, strongly expressed even around the anterior margins of the diductor scars; scars directed away from each other initially, but tending to be parallel in the adult stage, extending to about midlength; widest part of the scars situated anterior to their midlength; each scar tapered anteriorly. Adductor scars elongate-ovate, completely enclosed by diductors and separated from them by a pronounced ridge. A thickened ridge extends around the valve inside the marginal deflexion, but not known in detail in the vicinity of the tongue. Denticulation and mantle canal system not known.

Interior of brachial valve (Pl. 50, fig. 6). Cardinal process lobes disjunct.

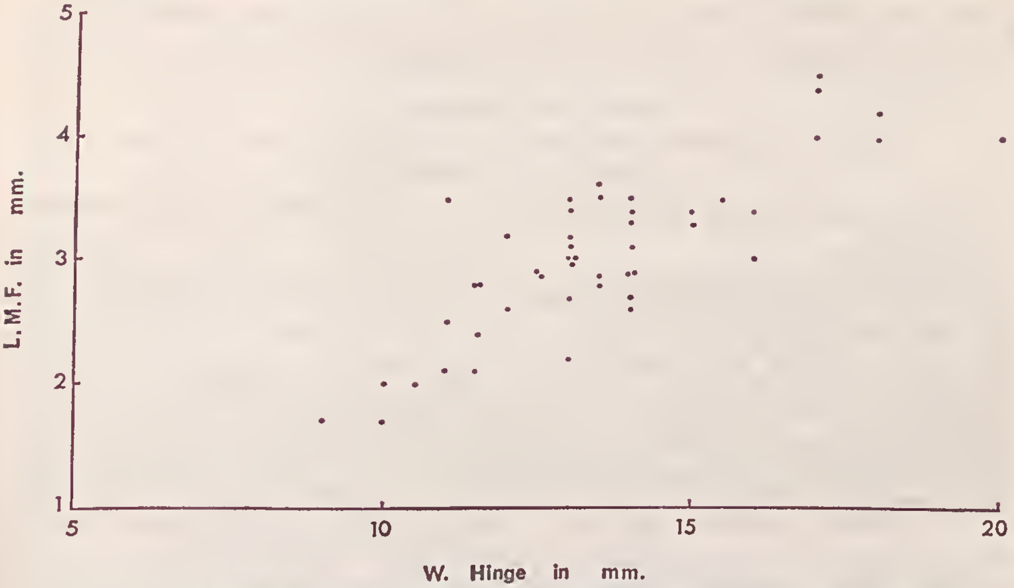

FIG. 7—Plot of Width of Hinge against Length of Muscle Field in the Pedicle Valve of *Malurostrophia flabellicauda.*

Lateral muscle-bounding ridge arcuate, concave on their outer margins, joined to the posterior thickened shelf paralleling the hinge line, but not joined to the median muscle-bounding ridges. Adductor scars roundly triangular. Transmuscle septa broad and slightly sinuous, median septum broad and forming a pronounced transversely oriented node. Inner surface anterior to the muscle field having a pronounced rounded ridge parallel to the margin and rising to a median node. Inner surface papillose, not showing impressions of the mantle canal system.

DIMENSIONS (mm): Two specimens from locality 16, Bindi, Victoria, have the following dimensions;

	Length	Width	Maximum height
Holotype (GSV 58553)	12·5	18·6+	8·4
Paratype (GSV 58554)	11·7+	16·0+	5·2

DISCUSSION: *M. basilica* differs from the type species of *Malurostrophia, M. flabellicauda,* in having less markedly parvicostellate ornament and a less fan-like arrangement of the costellae on the tongue. The lateral muscle bounding ridges of the brachial valve are more sinuous than in *M. flabellicauda,* and the transverse node delimiting the anterior adductor scars is more strongly expressed. Of obvious importance is the much greater size of *M. basilica.* It cannot be construed as having been based on grontic individuals of *M. flabellicauda* for geniculation occurs in the latter at c. 5 mm from the hinge line compared with at about 9 mm in *M. basilica*—i.e. at the same relative maturity *M. basilica* is an altogether more robust species.

LOCALITY: Known only from the Taravale Formation at locality 16, a washout on the south side of a gully draining to Junction Ck, 1,450 yards south-east of the Sugarloaf, Bindi, Victoria. This locality is about 1,700 ft above the top of the Buchan Caves Limestone and represents an horizon stratigraphically higher than that which yielded *M. flabellicauda* and *Calceola* at Buchan, perhaps 1,000 ft higher. Present evidence (Talent 1965) indicates that these beds are not older than Upper Emsian and are most probably Eifelian in age.

Functional Morphology

Evidence of Shell Orientation, Shell Attachment, and Feeding Currents

With regard to gross shape there are four growth stages to be functionally interpreted.

Stage 1. At the initial stage the shell was attached by a pedicle. As a result of incomplete silicification of the shell margins it is not possible to state with certainty the shell size limits within which the pedicle atrophied, but it is approximately at the period of initial geniculation. No pedicle sheaths have been observed but in several individuals the angle at which the pedicle passed through the shell can be determined. In shells which have not quite become geniculate the foramen occupies the tip of the umbo and the pedicle tube passes anteriorly through the test at a very low angle to the external shell surface (Pl. 48, fig. 17-18). This angle is much lower than that observed in certain species of *Leptaena* (Arber 1939, 1940). The natural position of a shell attached by a pedicle oriented in this direction would be with its brachial valve downwards. Assuming that a lophophore existed in this group and that it produced a pair of lateral incurrents and a median excurrent, such a position would be feasible provided the organisms were held free of the soft substrate by attachment to some hard object.

Stage 2. When the pedicle atrophied, the shells would subside preferentially on to their brachial valves because of their orientation while attached. Specimens that came to rest on their pedicle valves would either die because the valve edges would be in the substrate, or perhaps invert themselves by clapping the valves together. Since death would ensue for many, one would expect a mortality peak at this shell size. This is yet to be checked. Those oriented with the pedicle valve upwards would feed in the normal way, the entire shell edge being above the substrate. It is significant that ears began to appear on the hinge while the shell was still attached by the pedicle, and they continued to grow with positive allometry, thus providing some stability for the shell when it became free.

Stage 3. In young adults, though the lateral margins continue their ventrad growth, the median sector is reflexed dorsad and would thus tend to be immersed in sediment. Whilst this, together with the extended ears, would make for high stability, it would create problems with regard to the disposal of water in a median excurrent.

There is, however, evidence in both *Leptodontella* and *Malurostrophia* to suggest a modification of this current. The ventrad and subsequent dorsad deflexion of the median sector results in transverse lobation of this region, and in the formation of a pair of shallow channels directed laterally from the mid-line to the margins of the median deflexion (e.g. Pl. 47, fig. 16). In addition, *Malurostrophia* has these channels emphasized by the formation in the brachial valve of a sharp triangular median node with a distinct posterior ridge (Pl. 48, fig. 1, 11). Such an arrangement would split the median excurrent into two, allowing it to pass out on the flanks of the tongue above the substrate; it would also account for the break in the internal marginal ridge in the pedicle valve of most specimens where it commences to cross the tongue (Pl. 47, fig. 14; Pl. 49, fig. 4-8). The ridge is continued across in some individuals, but even in these it weakens at the edge of the tongue.

At this growth stage the extended hinge region becomes tubular (Pl. 47, fig. 12-16; Pl. 48, fig. 15-16) and it has been suggested (Orton 1914; but *cf.* Rudwick 1960) that in some genera these tubes may have been feeding devices. Such a view cannot be supported. The orifices at the ends of the hinge would tend to be submerged, and in any case the internal marginal ridge constricts the tube where the two structures intersect. The tubes were more probably the sites of strong vascular trunks for carrying coelomic fluids to the ears, which were very active regions of shell deposition, that is, they were deeply impressed pallial markings. Some credence is lent to this view by the wealth and strength of the trunks supplying the other rapidly growing edge, the median deflexion (cf. their density on the inner surface of the median deflexion, Pl. 47, fig. 16; Pl. 49, fig. 6-8, with those on the marginal deflexions, Pl. 48, fig. 6 and Pl. 49, fig. 7).

Stage 4. In the oldest specimens the lateral margins in front of the ears are reflexed dorsally, leaving only the sectors on either side of the median deflexion directed ventrally. On the interior of the pedicle valve the axis of this reflexion is accompanied by slight thickening, and this sector is thus effectively sealed. Only the areas of water intake are then left standing above the substrate. The reflexed areas presumably provide additional stability.

If our discussion of the relationships of *Malurostrophia* and *Leptodontella* is correct this remarkable series of adaptations has been independently developed in the two genera. They have also been developed independently (Pl. 49, fig. 9-11) in the genus *Notoleptaena* Gill (= *Rugoleptaena* Havlíček). The functional significance of the external shapes of these genera has been discussed by Gill (1951, p. 196-199) and Kozlowski (1929, p. 92), both of whom believe that the shells rested on their pedicle valves, the lateral margins serving as an anchor and the tongue permitting the access of clear water. Gill apparently concluded that the incurrents were sited on the flanks of the tongue and that the excurrent was medial. Such an arrangement seems to us to be less likely than that suggested above because of

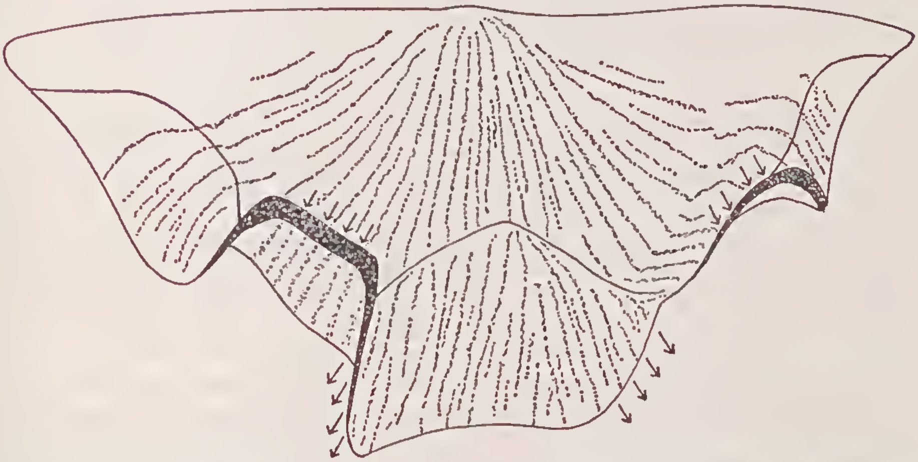

FIG. 8—Outline diagram of *Malurostrophia flabellicauda* with the valves slightly separated. Arrows indicate inferred positions of in-and excurrents.

(1) the deflecting structures in the median line; (2) the difficulty of separating in- and excurrents on the inner surface of the tongue; (3) the highly significant dorsad deflection of part of the lateral margins in Stage 4 of *Malurostrophia* and *Notoleptaena* (Kozlowski 1929, Pl. 3, fig. 24a, b), isolating a well defined intake sector on each side of the tongue.

Evidence of the Structure and Position of the Lophophore and the Viscera

In reconstructing the soft part morphology there are several points to be made initially: (1) The muscles of brachiopods lie within the coelomic cavity, and therefore the inner epithelium of the mantle must pass in front of the anterior edges of the muscle scars. (2) In living articulates, the coelomic cavity is short relative to the total length of the shell, but the high convexity of the shells allows it considerable depth. In plano-convex or concavo-convex shells with a comparable shell surface area (and presumably comparable food and oxygen requirements), the coelomic cavity would have to be relatively longer in order to produce a comparable volume. (3) In living brachiopods, the viscera usually lie suspended behind, between and sometimes partly in front of the adductor muscles. They are usually close to the brachial valve, the stomach being situated behind the mouth which is placed in the brachial groove at the junction of the two arms of the lophophore. The stomach is suspended in position by the gastro-parietal and ilio-parietal bands, and by dorsal and ventral mesenteries. The dorsal is usually the stronger of the two mesenteries, and according to Hancock (1859, p. 813) in the terebratellacean *Waldheimia* 'extends from the dorsal face of the stomach and anterior wall of the chamber to its upper wall, running along from end to end of the septum of the dorsal valve'. The gastro-parietal bands extend backwards to the adductor muscles, and the ilio-parietal bands run laterally to meet the walls of the coelomic cavity at varying positions and over varying distances according to the genus concerned. In addition there is usually a median gastro-parietal band which in *Waldheimia* meets 'the dorsal wall a little in advance of the hinge-plate' (Hancock, p. 813).

Errors in the interpretation of the soft parts of extinct concavo-convex brachiopods have been made in the past by the failure to consider the two valves together. Hollow specimens and thin sections of *Malurostrophia* have shown that: (a) The anterior parts of the transmuscle septa of the brachial valve lie opposite or just lateral to the inner muscle bounding ridges of the pedicle valve, i.e. they lie opposite the inner anterior edges of the diductor muscles (Fig. 1). (b) The so-called brachial ridges (lateral brachial ridges of Harper *et al* 1966) lie opposite the outer anterior part of the diductor muscle bounding ridges in the pedicle valve; and the posterior muscle bounding ridges in the brachial valve are almost flush up against the everted edges of the diductor muscle bounding ridges in the pedicle valve. (c) The anterior tip of the breviseptum of the brachial valve lies approximately in line with the anterior tips of the diductor scars in the brachial valve.

Similar relationships may be observed in other shallow-bodied stropheodontids such as *Nadiastrophia*, *Leptodontella*, and *Zophostrophia* in which these structures are present, but they do not hold for deep-bodied genera.

The opposing relationships of the transmuscle septa and so-called brachial ridges of the brachial valve, and the diductor muscles and muscle bounding ridges of the pedicle valve, indicate that they did not support the lophophore. On the other hand, the transmuscle septa and the inner diductor bounding ridges outline a cavity which is appropriately placed to contain the stomach and intestine, with the dorsal median septum (breviseptum) marking the line of junction between the dorsal mesentery and the outer epithelium. The mouth would be situated near the anterior end of the breviseptum, which is elevated to act as a support for this region where the unsupported lophophore joins the diaphragm. The ilio-parietal bands were probably attached to the wall of the coelomic cavity along the transmuscle septa, and the small triangular median scar at the rear end of the dorsal breviseptum may mark the area of attachment of the median gastro-parietal band. On this interpretation the 'lateral brachial ridges' would demarcate part of the line along which the inner epithelium turned ventrad to form the wall of the coelomic cavity. The space between the transmuscle septa and the 'lateral brachial ridges' would be occupied, at least in part, by lateral digestive diverticula. If this interpretation be true, the mantle cavity was deeply divided and really consisted of two chambers with maximum height in front, decreasing gradually in height toward the rear where its shape is effectively outlined by the thick marginal ridges. The two chambers are joined by a short passage in front of the mouth.

What feeding devices could utilize a mantle cavity of this shape? There seem to be three possibilities—the circulation of water by rapid opening and closing of the valves and the subsequent entrapment of food particles on mantle cilia which then passed them to the mouth via ciliated mantle tracts; the production of in- and excurrents and the entrapment of food particles by tracts of mantle cilia; and lophophore feeding.

Both of the mantle feeding mechanisms have been rejected. No living forms feed exclusively by mantle cilia. Rudwick (1961, and in Moore 1965), however, has suggested that richthofeniids used a rapid opening and closing valve mechanism to induce water circulation, food particles being caught on the mantle and perhaps a modified lophophore; and he has further suggested that 'a similar feeding process could have been utilized by many less aberrant productoids, and may even have been characteristic of the whole group'. It seems an unlikely interpretation for *Malurostrophia* because of its very flat mantle cavity which *a priori* would seem not to permit the generation of the necessary eddy currents, the posterior part of the mantle cavity would be 'dead-space', and water would be sucked into the mantle cavity around the entire shell margin including the sectors buried in the substrate. Confirmation of these views by the use of models is desirable. The formation of feeding currents by ciliary tracts on the mantle is improbable because such currents would be very weak, and in any case, there would be no possibility of separating filtered from non-filtered water.

Lophophore feeding is the only remaining possibility. At the early growth stages there seems to be no reason why a trocholophe should not have been present. In living brachiopods these types occur only in juveniles or in small adults. A median incurrent is produced and lateral excurrents pass out around the shell edge, the median incurrent being made possible by a wide shell gape. This could occur in *Malurostrophia* up to the stage of shell deflexion, but beyond that the shape of the median deflexion would obstruct any median incurrent. In any case, if the inferences made from gross shell shape concerning the direction of currents in adults are reliable, the mantle cavity would have to be divided into lateral inhalant chambers and a median exhalant chamber. In living brachiopods such an organization is present only with zygolophous, plectolophous or spirolophous lophophores. A plectolophe could not effectively occupy a mantle cavity of the *Malurostrophia* type, even allowing that the median spiral could be accommodated.

Recently Cowen and Rudwick (1966) have demonstrated the existence of spiral brachidia in the Jurassic strophomenoid *Cadomella*, which they regard as closely allied to the concavo-convex Mesozoic spire bearers of the Koninckinidae. The spires in these forms are very flat and are ventrally directed. The possibility of a similar spirolophe having been present in *Malurostrophia* must be seriously considered, though it is not necessary to conclude that because the members of one small family of Strophomenida bore spirolophes, those of all the other constituent groups did likewise. The Koninckinacea is thought to be a Mesozoic offshoot from the Chonetacea, a superfamily that was already distinct from the Strophomenacea (to which *Malurostrophia* belongs) in the late Ordovician. This long independent history leaves ample scope for the development of diverse characters and in this respect it is important to note that not all the Koninckinacea have the typical strophomenidine shell tissue structure. Only the Koninckinacea among the Strophomenidina survived the end of the Palaeozoic, and it is not impossible that it was the assumption of a spirolophe that enabled them to succeed.

The mantle cavity in *Malurostrophia* was only about 1 mm high in adults with the shell closed. There is no evidence that the shell gaped widely during feeding; on the contrary, the geometry of the marginal deflexions and internal ridges suggests

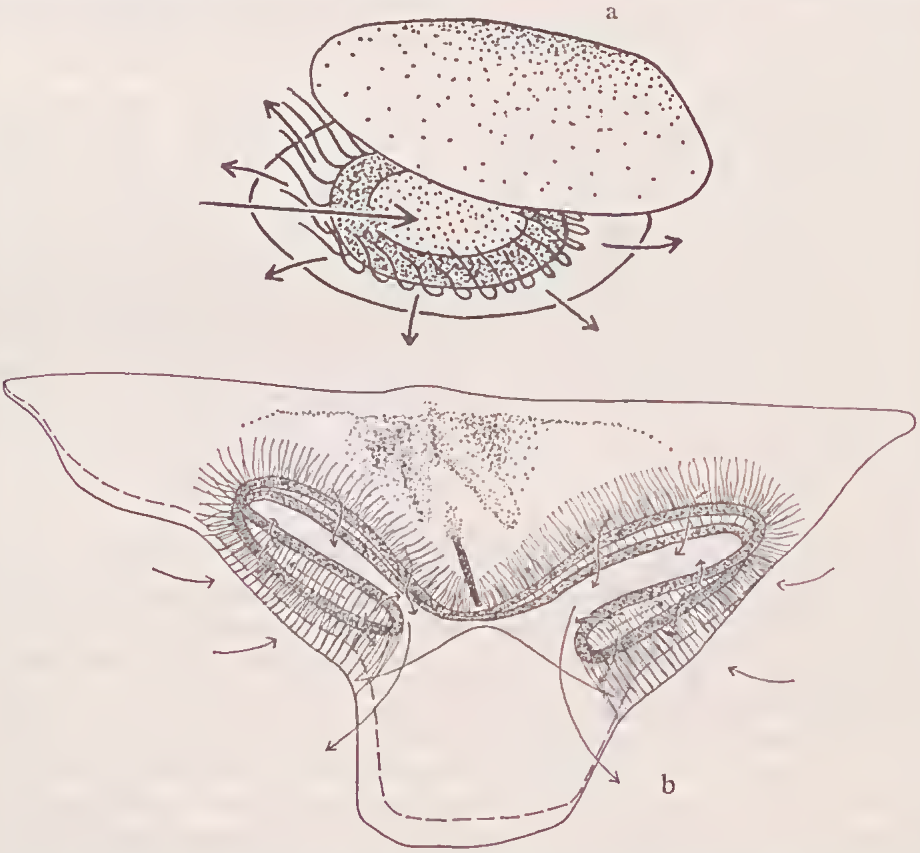

FIG. 9—(a) Reconstruction of the trocholophous early growth stage of *Malurostrophia flabellicauda*. (b) Reconstruction of the zygolophous adult stage showing the disposition of the lophophore and the flow pattern of the feeding currents. Upper (pedicle) valve outlined by dashes.

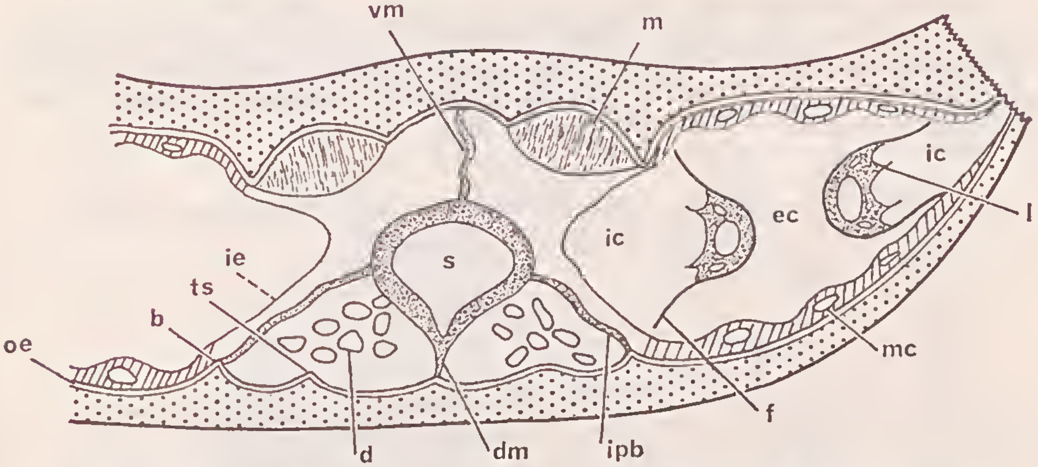

FIG. 10—Diagrammatic reconstruction of a transverse section taken across *Malurostrophia flabellicauda* between the anterior edges of the adductor and diductor muscles in the pedicle valve. b = 'lateral brachial ridge'; d = digestive diverticula; dm = dorsal mesentery; ec = exhalant chamber of mantle cavity; f = filament of lophophore; ic = inhalant chamber of mantle cavity; ie = inner epithelium of mantle; ipb = ilio-parietal band; l = lophophore lip; m = diductor muscle; mc = mantle canal; oe = outer epithelium; s = stomach; ts = transmuscle septum; vm = ventral mesentery.

that the gape was slight. In any case, even if it reached 25°, the maximum height of the mantle cavity in life would have been less than 1·5 mm, and that towards its front. The ventral surface of each mantle cavity would have been rather flat and not arched to receive the apex of a spire. Each chamber would also be only 2·0-2·5 by 4·0-4·5 mm in most adults. A spire occuping a cavity with these dimensions would be similar in size to those formed shortly after metamorphosis from a schizolophe in modern rhynchonellaceans (Rudwick 1962). Further, a spire effectively occupying a cavity with such an irregular bean-like outline (see Pl. 47, fig. 15) would need a more complicated outline than that of such forms as *Cadomella*.

None of these objections to a spirolophe is conclusive. On the other hand there is no really persuasive evidence in favour of such a reconstruction, either for *Malurostrophia* or for any other Palaeozoic Strophomenacean. However, another reconstruction commends itself more than does a spirolophe. A zygolophe oriented in the manner shown in Fig. 9 would satisfy all the known requirements. Its maximum incurrent and excurrent pressures would be appropriately placed, the flat bean-shaped mantle chambers would be effectively occupied, the inhalant and exhalant chambers would be neatly separated, the brachial arms would be free of valves and leave no impression on the shell, and the high point at the anterior end of the median septum could be interpreted as their only support (apart perhaps from spicules). The size of the shell is no objection, since in recent genera zygolophes are known, even in such deep bodied forms as *Fallax*, at shell lengths up to 54 mm (Atkins 1960). The fact that zygolophes are at present known only in the Terebratulida is not regarded as contrary evidence, since the more complex spirolophe is known to have developed independently at least three times, and our knowledge of two of these evolutionary events is based on rarely occurring early Mesozoic genera (Cowen & Rudwick 1966, p. 406).

This interpretation differs fundamentally from that offered by Williams (in Moore 1965) and Harper *et al* (1966) for genera of the Strophomenacca. Application of a similar line of argument would also require drastic revision of the lophophore reconstructions of some of the productaceans and plectambonitaceans offered by Williams & Rowell (in Moore 1965, p. 107).

TABLE 1

Dimensions (mm) of Malurostrophia flabellicauda *sp.nov., arranged in growth series*

A. BIVALVED SPECIMENS

Length	Breadth	Height Tongue	Height ped. interarea	Height br. interarea
1. *Receptaculites* Limestone, Bloomfield Station, Taemas, N.S.W.				
5·8	8·4	1·9	0·35	0·22
6·1	11·4	—	0·45	0·25
7·0	11·0	3·6	0·55	0·32
7·4	10·8	4·0	0·55	0·32
7·4	11·0	4·2	0·60	0·35
7·8	11·4	4·0	0·55	0·30
2. Crinoidal Limestone, Hume Park, N.S.W.				
6·2	9·8	4·7	0·50	0·2+
6·6	11·0	5·0	0·55	0·25
3. Murrindal Limestone, Rocky Camp Ridge, Buchan, Victoria				
4·5	7·6	—	—	0·20
4·5	7·8	1·7	—	—
4·5	8·2*	3·2	0·40	0·15
4·8	8·4*	2·1	0·30	0·20
5·1	8·9	2·1	0·35	0·20

B. ISOLATED PEDICLE VALVES—*Receptaculites* Limestone, Bloomfield Station, Taemas, N.S.W.

Length	Breadth	Width of Denticulation Ped. Valve	Max. Length Muscle Field Ped. Valve	Max. Width Muscle Field Ped. Valve	Length Hinge to Median Node	Length Adductors	Width Adductors
—	5·3	2·2	0·8	1·1	—	—	—
—	7·2	3·2	1·3	1·6	4·0	—	0·6
—	a8	3·6	1·6	2·0	4·3	0·7	1·0
6·0	a10	5·5	2·7	2·3	4·0	1·4	1·2
6·0	10·5	5·2	2·1	2·4	4·3	1·0	1·1
6·5	a12	6·2	2·6	2·3	4·3	1·2	1·3
6·5	12·0	7·0	2·8	2·7	4·5	1·6	—
7·0	12·5	6·5	3·3	3·1	4·5	1·2	1·5
7·2	12·8	5·1	2·5	2·5	4·9	1·1	1·0
7·5	12·4	6·6	3·2	2·8	4·8	—	1·3
7·5	12·5	6·5	3·1	2·7	4·6	1·3	1·2
7·5	14·4	—	3·4	3·2	5·0	—	1·4
8·0	a13	7·6	3·5	2·7	5·0	1·2	1·5
8·0	15·0	7·0	2·7	2·7	5·5	1·7	1·2
8·2	a20	9	4·0	3·2	6·0	1·8	2·0
8·5	a17	8·5	4·0	3·5	5·2	1·5	1·4

C. ISOLATED BRACHIAL VALVES—*Receptaculites* Limestone,
Bloomfield Station, Taemas, N.S.W.

Length Hinge to Point of Deflection	Breadth	Height Tongue	Width Cardinal Process Lobes	Width Muscle Field of Br. Valve	Length Hinge to Anterior end of Ant. Adductors	Length Socket Plates	Length Strongly Expressed Muscle-bounding Ridges
—	5·3	—	$0{\cdot}1_2$	1·1	a2·0	0·2	$0{\cdot}2_5$
—	$5{\cdot}1_5$	—	$0{\cdot}1_2$	—	—	0·3	0·3
—	—	—	$0{\cdot}2_2$	1·1	2·9	0·5	0·6
5·3	—	2·5	$0{\cdot}5_0$	1·9	3·7	1·1	1·1
5·5	10·9*	1·0	$0{\cdot}4_2$	$1{\cdot}9_5$	3·3	1·1	0·9
5·0	—	2·2	$0{\cdot}3_5$	2·0	a4·0	1·0	$1{\cdot}0_5$
5·1	11·4*	1·9	$0{\cdot}6_2$	$2{\cdot}0_5$	—	1·0	1·0
5·0	11·9	—	$0{\cdot}4_5$	2·0	3·5	1·0	1·0
5·3	11·4*	2·6	$0{\cdot}5_5$	—	—	0·8	1·1
5·3	11·4*	2·3	$0{\cdot}5_0$	2·1	4·1	0·8	1·1
5·7	—	1·9	$0{\cdot}4_5$	2·2	3·6	0·8	1·2
—	—	—	$0{\cdot}5_5$	2·2	—	1·0	1·2
5·0	—	—	$0{\cdot}4_0$	$2{\cdot}2_5$	3·6	1·0	1·2
5·0	—	2·7	$0{\cdot}5_0$	2·1	3·9	1·2	1·1
5·6	12·2	2·6	$0{\cdot}7_0$	2·3	4·1	1·2	1·3
—	12·5*	—	$0{\cdot}4_5$	2·3	4·0	1·2	$1{\cdot}2_5$
5·2	12·8*	3·7	$0{\cdot}6_0$	2·7	3·8	1·2	$1{\cdot}1_5$

a = approximate
* = measurement of breadth derived by doubling measurement from midline to an unbroken alation

References

Arber, M. A., 1939. The nature and significance of the pedicle-foramen of *Leptaena* Dalman. *Geol. Mag.* 76: 82-92.

————, 1941. The relation of the valves to the pedicle in the strophomenoid brachiopods. *Ibid.* 77: 161-174.

Atkins, D., 1960. A new species and genus of brachiopod from the Western Approaches, and the growth stages of the lophophore. *J. mar. biol. Assoc. U.K.* 39:71-89.

Browne, Ida A., 1959. Stratigraphy and structure of the Devonian rocks of the Taemas and Cavan areas, Murrumbidgee River, south of Yass, N.S.W. *J. Proc. Roy. Soc. N.S.W.* 92: 115-128.

Cowen, R., & Rudwick, M. J. S., 1966. A spiral brachidium in the Jurassic chonetoid brachiopod *Cadomella*. *Geol. Mag.* 103: 403-406, Pl. 1.

Gill, E. D., 1951. Two new brachiopod genera from Devonian rocks in Victoria. *Mem. Nat. Mus. Vict.* 17: 187-205, Pl. 1.

Harper, C. W., Johnson, J. G., & Boucot, A. J., 1967. The Pholidostrophiinae. *Senck. leth.* 47 (in press).

Hancock, A., 1859. On the organization of the Brachiopoda. *Phil. Trans. Roy. Soc.* 148: 791-869, Pl. 52-65.

Havlíček, V., 1963. Čeléd Leptaenidae (Brachiopoda) v Českém Siluru a Devonu. *Čas. národ. Mus.* 102: 220-225, Pl. 1-2.

Kozlowski, R., 1929. Les brachiopodes gothlandiens de la Podolite polonaise. *Palaeont. polonica* 1: 1-254, 12 Pl.

Moore, R. C. (ed.), 1965. Treatise on Invertebrate Paleontology (H) Brachiopoda. Geol. Soc. Amer. & Univ. Kansas Press.

Orton, J. H., 1914. On ciliary mechanisms in brachiopods and some polychaetes, etc. *J. mar. biol. Assoc. U.K.* 10: 283-311.

Rudwick, M. J. S., 1960. The feeding mechanisms of spire-bearing fossil brachiopods. *Geol. Mag.* 97: 369-383.

———, 1961. Filter-feeding mechanisms in some brachiopods from New Zealand. *J. linn. Soc. London (Zool.)* 45: 592-615.

Schmidt, W. E., 1913. Cultrijugatuszone und Unteres Mitteldevon südlich der Attendorn-Elsper Doppelmülde. *Jahrbuch König. Pr. Geol. Land. zu Berlin* 33 (2): 265-318, Pl. 22-23.

Spriestersbach, J., 1925. Die Oberkoblenzschichten des Bergischen Landes und Sauerlandes. *Jahrbuch Pr. Geol. Land. zu Berlin* 45: 367-450, Pl. 10-17.

Talent, J. A., 1963. The Devonian of the Mitchell and Wentworth rivers. *Mem. Geol. Surv. Vict.* 24: 1-118, 78 Pl.

———, 1965. The stratigraphic and diastrophic evolution of central and eastern Victoria in Middle Palaeozoic times. *Proc. Roy. Soc. Vict.* 79 (1): 179-195.

Teichert, C., & Talent, J. A., 1958. The geology of the Buchan area, East Gippsland. *Mem. Geol. Surv. Vict.* 21: 1-56.

Williams, A., 1953. North American and European stropheodontids: their morphology and systematics. *Mem. Geol. Soc. Amer.* 56: 1-67, 13 Pl.

Explanation of Plates

The symbol ANU refers to collections of the Department of Geology, School of General Studies, Australian National University, Canberra; GSV refers to the fossil collections of the Geological Survey, Mines Department, Melbourne.

Plate 47

Fig. 1-5, 8-16, × 4; Fig. 6, 7, × 3·4.

Fig. 1-16—*Malurostrophia flabellicauda* gen. et sp. nov. 1-3, 6—dorsal, ventral, posterior and antero-ventral views respectively of holotype, ANU 14620. 4, 5—ventral and dorsal views respectively, ANU 14623; note the dorsal node and the greater density of costellation on the tail. 7—antero-dorsal view, ANU 14639. 8-15—growth series of pedicle valves, ANU 14630, 14629, 14633, 14627, 14628, 14622, 14624, 14614 respectively, showing the lack of defined musculature in the smallest available specimens, the cordate muscle field with diductors initially directed at right angles to each other but tending progressively towards sub-parallelism, the presence of a defined ventral process even in juvenile specimens, and the presence of strong vascula dentalia and a well defined marginal ridge on the interior of mature specimens (Fig. 13-15). 16—oblique postero-dorsal view, ANU 14635 to show the greater density of grooves on the inner surface of the tail compared with that of the ventrally deflected antero-lateral margins.

All specimens from the *Receptaculites* Limestone, Bloomfield Station, Taemas, N.S.W.

Plate 48

Fig. 1-3, 5-10, 12-16, 19-20, × 4; Fig. 4, × 6; Fig. 11, × 3·4;
Fig. 17, × 20; Fig. 18, × 25.

Fig. 1-20—*Malurostrophia flabellicauda* gen. et sp. nov. 1-2—antero-lateral and internal views of a large brachial valve showing the high antero-median thickening, ANU 14983. 3, 4—internal and posterior views of a gerontic brachial valve showing the thickened adductor scars and a small median scar, and the posterior face of the cardinal process and chilidium, ANU 14986. 5, 9, 12-14—internal views of four brachial valves showing variations in the differentiation of the adductor scars and size and outline of the transmuscle septa; 14 is the youngest individual, ANU 14985, 14619, 14982, 14617, 14625. 6—lateral view of part of 7 to show the pallial markings. 10—posterior view of 9. 11—anterior view of a gerontic individual showing the high antero-median thickening, ANU 14653. 15-16—internal and postero-lateral views of a large pedicle valve showing the reflected margins in front of the ears, ANU 14989. 17—dorsal view of a small individual showing the pedicle foramen, ANU 14993a. 18—internal view of a small individual in which the shell has been partly removed to expose the pedicle tube, ANU 14993b (subsequently broken). 19, 20—lateral and oblique views of a large complete individual to show the gross shape, ANU 14990.

All specimens from the *Receptaculites* Limestone, Bloomfield Station, N.S.W.

Plate 49

Fig. 1-2, × 10; Fig. 3, × 23; Fig. 4-8, × 4; Fig. 9-11, × 1·5.

Fig. 1-8—*Malurostrophia flabellicauda* gen. et sp. nov. 1-3—stereo-pairs of cardinalia and

muscle-bounding ridges of young specimen, ANU 14625, and mature specimen, ANU 14619; and postero-dorsal view of cardinal process lobes and palintrope of mature specimen, ANU 14626; note the dentition resembling a slotted groove (Fig. 2), the narrow notothyrium covered by the concave chilidium (Fig. 3), and the lobate nature of the attachment faces of the cardinal process lobes (Fig. 2 & 3). 4-8—oblique posterior and lateral views of four pedicle valves to show the variation in shape of the muscle field, the everted muscle bounding ridges, the mantle canal system, particularly the vascula dentalia and the vascula media; Fig. 4, 8, ANU 14622, Fig. 5, ANU 14621, Fig. 6, 7, ANU 14987.

Fig. 9-11—*Notoleptaena* sp. nov. 9-10—dorsal and oblique views of an almost complete specimen, GSV 61828. 11—ventral view of a partly eroded specimen, GSV 61829.

M. flabellicauda from *Receptaculites* Limestone, Bloomfield Station and *N.* sp. nov. from the Taravale Formation, locality 16, Bindi, Victoria (same locality as *M. basilica*).

PLATE 50

Fig. 1-7, 13, × 3·5; Fig. 8-10, × 5; Fig. 11, 12, × 1·5.

Fig. 1-7—*Malurostrophia basilica* gen. et sp. nov. 1-5—dorsal, ventral, posterior, lateral, and anterior views respectively of holotype GSV 58553; note the grooving of the dorsal and ventral palintropes corresponding to the dentition, and the less parvicostellate ornament compared with *M. flabellicauda*. 6—internal mould of brachial valve of paratype GSV 58554 prepared by calcining and scraping; note the general resemblance to the brachial interior of *M. flabellicauda* except for the more sinuous transmuscle septa (brace plates). 7—internal mould of pedicle valve of same specimen, prepared by calcining and scraping; note the strong ridges bounding the adductor muscle field.

Both specimens from the Taravale Formation, locality 16, Bindi, Victoria.

Fig. 8-10—*Malurostrophia flabellicauda* gen. et sp. nov. 8, 9—ventral and oblique lateral views of GSV 58552; note the pronounced costellation and the prominent median node; 10—ventral view of GSV 58551; note the primary deformation of the specimen.

Both specimens from the *Calceola* band of the lower Murrindal Limestone on the crest of the ridge running east from Rocky Camp, Buchan, Victoria.

Fig. 11-13—*Leptodontella caudata* (Schnur). 11—plaster replica (internal mould) of pedicle valve, GSV 58549—original in the Schultz Collection, Museum of Comparative Zoology, Harvard University, U.S.A.; contrast the flabellate musculature with that of *M. basilica* (Fig. 7) and *M. flabellicauda* (Pl. 1 and 2). 12, 13—rubber mould of brachial interior, and enlargement of musculature and cardinalia, GSV 58550—original in the collections of the U.S. National Museum, Washington, U.S.A.; contrast the musculature and muscle-bounding ridges with those of *M. basilica* (Fig. 6) and *M. flabellicauda* (Pl. 2).